BASAL METABOLIC RATE AND ENERGY EXPENDITURE DURING INCUBATION IN THE WANDERING ALBATROSS (*DIOMEDEA EXULANS*)

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ABSTRACT.—Metabolic rates of incubating and non-incubating adult Wandering Albatrosses (*Diomedea exulans*) were measured using the birds' rate of oxygen consumption. Basal metabolic rate (BMR) was 1,755 kJ day^{-1} for birds of mean mass 8,130 g. This is close to the BMR predicted for non-passerines of equivalent mass from allometric equations. Incubating female Wandering Albatrosses of mean mass 7,930 g expended 2,415 kJ day^{-1}. This is 1.4 times BMR, and is also higher than previous estimates for incubating Wandering Albatrosses based on their rates of mass loss. These differences may be due in part to stresses imposed on the incubating birds during measurement of oxygen consumption, or to errors in estimating the amount of fat that the birds oxidized during their incubation fast, in studies where their energy expenditure was calculated from loss of mass.

Procellariiform birds have long incubation periods with long individual incubation shifts during which they fast (Lack 1968, Whittow 1980). Their energy expenditure during incubation can be estimated from their loss of mass, provided the foodstuffs that they oxidize during the fast are known (Croxall 1982). Rates of metabolism have been measured in several species using this technique (reviewed by Croxall 1982). Wandering Albatrosses (*Diomedea exulans*) have among the longest incubation periods of any procellariiforms (78 days), with individual shifts that are up to 12 days long (Croxall, in press) and probably up to 30 days under exceptional circumstances (Van Zinderen Bakker 1971). Croxall and Ricketts (1983) have estimated energy expenditure of incubating Wandering Albatrosses from changes in the birds' mass. An alternative, and potentially more accurate method of estimating energy expenditure is to measure the rate of oxygen consumption of incubating birds on the nest (e.g., Ricklefs 1974, Gessaman and Findell 1979). To date, oxygen consumption of incubating birds has been measured in only two species of procellariiforms (Grant and Whittow 1983).

At Marion Island, several pairs of Wandering Albatrosses nest close to the meteorological station. They show little fear of man and are relatively tolerant of experimental manipulation. Consequently, they are ideal candidates for field measurements. In this study, we report on their basal metabolic rates (BMR) and the energy that they expend during incubation from measurements of their oxygen consumption.

METHODS

MEASURING THE BMR OF ALBATROSSES

We measured the BMR of two male and two female Wandering Albatrosses at sub-Antarctic Marion Island (46°52'S, 37°51'E), using their rates of oxygen consumption ($\dot{V}_{O_2}$). These were measured in a translucent, airtight metabolic chamber (74 l in volume), using a pump-driven, open-flow system coupled to a Taylor Servomex OA 570 paramagnetic oxygen analyzer. Air was pumped through the chamber, a tube of silica gel, a Rotameter flowmeter, and a tube of silica gel/carbosorb before entering the oxygen analyzer. The flow rate was 3–4 l min^{-1}, which produced a drop in oxygen content in the outflow air of 1–2% below that of ambient air. The oxygen content of ambient air was assumed to be 20.9% and was checked periodically throughout each determination. The temperature inside the chamber was measured with a mercury thermometer or a thermocouple. Temperature, flow rate, and the percentage of oxygen in the outflow air were recorded at 30-min intervals over 24 h under natural photoperiodic conditions. We allowed 2 h for the birds to settle and to equilibrate thermally with chamber air before taking the first readings.

The temperature inside the chamber could not be controlled during the study, but it remained within a range (2.2–16.0°C, mean 11.6°C) that the birds normally experience under natural conditions. The lower critical temperature of the Wandering Albatross is not known, but that of the sympatric King Penguin (*Aptenodytes patagonicus*), an approximately
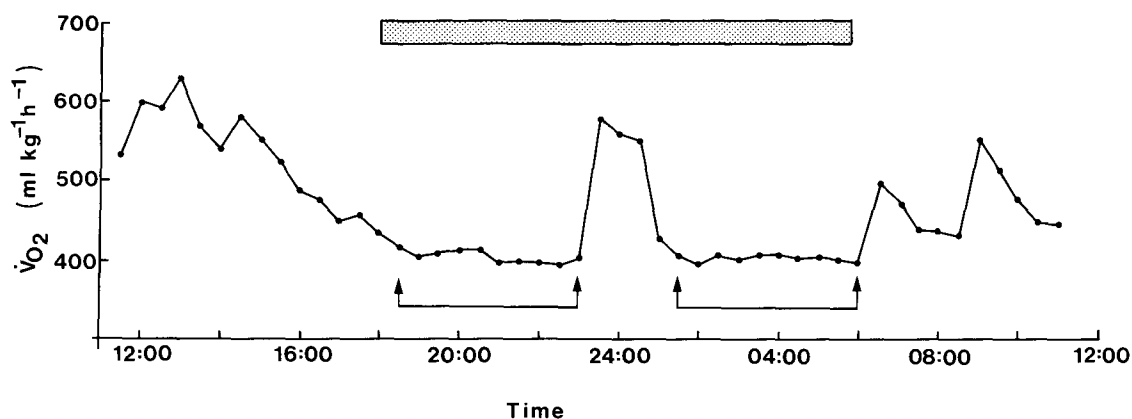
FIGURE 1.   Mass-specific metabolic rate ($\dot{V}_{O_2}$) of an adult Wandering Albatross over 24 h under normal photoperiodic conditions at Marion Island. The stippled bar indicates hours of darkness; segments between connected arrows are the stable periods from which this bird's BMR was calculated.

12,000-g bird, is $-5°C$ (Le Maho 1977). By analogy, we assumed that the lower critical temperature of the Wandering Albatross was likely to be below $2.2°C$ and that the birds were within their thermoneutral zone. Supporting this assumption was our observation that chamber temperature and the mass-specific metabolic rate of the birds were not significantly correlated over the temperature range of the experiment ($r = -0.18$, $P > 0.1$, $n = 18$). For this reason, we have used the term BMR, as defined by Kendeigh et al. (1977).

MEASURING THE METABOLIC RATE OF
INCUBATING WANDERING ALBATROSSES

Wandering Albatrosses at Marion Island lay their eggs from 27 December to 9 January (Van Zinderen Bakker 1971). We did not begin our experiment until at least three weeks after that (2 February) in order to minimize the risk of nest desertion. This precaution proved adequate, since none of the experimental birds deserted their nests. Although we intended to use both sexes, the males were more aggressive and often moved off the nest when we placed a mask on them. For this reason, we confined our study to females, which tolerated a mask well.

We measured the metabolic rate of five different incubating females using an open-mask system described by Withers (1977). We measured metabolic rate once only on two of the birds, twice on another two birds, and on four different occasions over a period of four weeks on the remaining bird. The mass-specific metabolic rate did not differ significantly between the first and last sessions in any of the birds in which we measured metabolic rate more than once (student's t-test).

We constructed the mask from a soft, plastic, 1-l reagent bottle. The base was cut to fit the contours of the bird's face and bill, and was lined with foam-rubber to prevent abrasion on the bird. The air line was inserted into the neck of the bottle through a rubber bung and the mask was held in position on the bird with an elastic strap. The mask was designed to fit snugly over the bill, but not the eyes, since obstructing the bird's vision agitated it and made it reluctant to settle on the nest. Air was drawn past the bird's face by a pump situated in a tent nearby. The relatively small differences between the oxygen content of inflowing and outflowing air due to high flow rates are a potential source of error when a mask is used to measure metabolic rate. However, low flow rates would subject the animal to unacceptably low levels of oxygen (Withers 1977). Consequently, we maintained the air flow at 30–40 $l\ min^{-1}$ with a flowmeter placed upstream of the pump. The air was passed through two tubes of silica gel/carbosorb before entering the oxygen analyzer.

The high flow rate and the small volume of dead air space within the system ensured rapid equilibration and prevented backflow or leakage of effluent air. Readings of the oxygen content of the outflow began once we saw the bird settle on the nest. Thereafter, readings were taken every 5 min for 1–4 h. The birds were watched continuously from the tent and any activity on the nest was immediately apparent. Increases in the bird's oxygen consumption associated with visible activity were omitted when we later calculated energy expenditure. The oxygen content of ambient air was checked periodically during the run and air temperature was measured every 30 min. The latter ranged from 3.5 to $11.7°C$ (mean $8.6°C$). In-

TABLE 1.   Basal (BMR) and average daily (ADMR) metabolic rates of Wandering Albatrosses. Values for mass and measured metabolic rates are $\bar{x} \pm$ SD.

| | n | Mean mass (g) | Measured BMR | | Measured ADMR | | Predicted BMR[a] (kJ day^{-1}) | Measured BMR/ predicted BMR |
			(kJ day^{-1})	(kJ kg^{-1} day^{-1})	(kJ day^{-1})	(kJ kg^{-1} day^{-1})		
Adults (male and female)	4	8,130 ±1,090	1,755 ±446	216	2,012 ±449	248	1,613	1.08
Incubating females	5	7,930 ±956	2,415[b] ±308	305	—	—	1,601	1.51

[a] From the allometric equation of Kendeigh et al. (1977): BMR = $0.522W^{0.7347}$ where W is a bird's mass in g and BMR is in kcal·day^{-1} (converted here to kJ·day^{-1}; 1 kcal = 4.184 kJ).
[b] Metabolic rate while incubating eggs.

cubation shifts in the Wandering Albatrosses may last up to 12 days (Croxall, in press), and we did not know how long the birds had been incubating when we made our measurements.

We calculated $\dot{V}_{O_2}$ (corrected to STPD) of non-incubating and incubating albatrosses with the equation of Hill (1972), for dry, CO_2-free air. We assumed that the lowest stable periods during each run represented the bird's BMR (Fig. 1) and the energy expenditure of incubating birds, respectively. Stable periods lasted from 3–12 h during our studies of BMR and 25–50 min during our measurements on incubating birds. If a bird exhibited more than one stable period during a session, we pooled the values of the periods to calculate its BMR or energy expenditure during incubation. Each $\dot{V}_{O_2}$ was converted to its energy equivalent using 1 1 O_2 = 20.083 kJ. Error estimates in this paper are ±1 SD.

RESULTS

We noted no consistent, well-defined phases of rest and activity, as described by Aschoff and Pohl (1970), in the metabolic activity of the Wandering Albatrosses. Two of the birds had low stable periods of metabolic activity during the day, one was least active at night (Fig. 1), and the fourth was least active during a period that lasted from 1 h before first light until midday. Albatrosses are active during the day, but probably feed at night (Imber and Berruti 1981), which probably accounts for the absence of well-defined activity patterns. Such patterns are also absent in several other nocturnal, as well as diurnal, species of procellariiforms (Adams and Brown, in press).

The mass-specific BMR's did not differ significantly between the sexes ($P > 0.1$, student's t-test), so we pooled the results. Measured BMR of the birds was only 8% greater than that predicted for birds of equivalent mass (Table 1). However, the mass-specific energy expenditure of incubating females was 1.4 times greater than that of the non-incubating albatrosses used in the laboratory studies ($P <$

0.001, student's t-test), and 1.5 times greater than their predicted BMR (Table 1).

Average daily metabolic rates of the albatrosses were 1.15 times their BMR. These may, however, be overestimates since three out of the four individuals had relatively high, but decreasing, rates of $\dot{V}_{O_2}$ for several hours after the first readings were taken (Fig. 1) and the birds may still have been stressed. Recalculation of average daily metabolic rates, excluding these periods, shows that the largest probable overestimate is 6%.

DISCUSSION

McNab (1966) and Warham (1971) suggested that procellariiform birds have lower metabolic rates than other non-passerines of similar size. The BMRs of Wandering Albatrosses in our study (Table 1) fail to support this idea, since they are nearly identical to the BMR predicted for birds of this mass by Kendeigh et al.'s equation (1977) for non-passerines. This is also the case for the BMR (calculated from $\dot{V}_{O_2}$ measurements) for nine other species of procellariiforms (Adams and Brown, in press). Average daily metabolic rates were up to 15% greater than BMR, which emphasizes the need for measuring metabolic rate over longer periods, as shown by Aschoff and Pohl (1970), when estimating BMR.

On the basis of loss of mass, Croxall and Ricketts (1983) estimated the energetic cost of incubation in the Wandering Albatross to be about 1.2 times the predicted BMR. Similar estimates, using the same technique, have been made for the Grey-headed Albatross (*D. chrysostoma*) and the Black-browed Albatross (*D. melanophrys*; Prince et al. 1981). Our estimate for incubating Wandering Albatrosses was somewhat higher, 1.4 times their measured BMR, although it was within the range calculated by Croxall (1982) for procellariiforms in general.

A fundamental problem in estimating energy expenditure from rates of mass loss is that either some knowledge is needed or some as-

sumptions must be made about the metabolites oxidized for energy. To our knowledge, this information is not available for procellariiforms. Therefore, general use has been made of data for incubating Emperor Penguins (*Aptenodytes forsteri*), in which 55.5% of the mass lost is fat, 9.2% is protein, and 35.5% water (Groscolas and Clement 1976). Using the mass-specific metabolic rate (kJ kg^{-1} day^{-1}) of our experimental birds (Table 1) and the mean mass of the incubating female Wandering Albatrosses from Croxall and Ricketts (1983), we could calculate a daily energy expenditure for their birds. We assumed that Wandering Albatrosses and Emperor Penguins metabolize protein at the same rate (9.2% of their daily mass loss) and subtracted the energy equivalent of this protein from the calculated daily energy expenditure in order to obtain the energy contribution of the fat. We divided this by the energetic value of fat (39.7 kJ g^{-1}) to obtain the amount of fat oxidized per day. Using this value and the daily mass loss of female Wandering Albatrosses (Croxall and Ricketts 1983), we estimated that 75% of the mass lost daily during the incubation fast is due to fat metabolism. Assuming that incubating male Wandering Albatrosses have metabolic rates that are similar to those of females, and using the mean mass and mass loss of incubating male albatrosses (Croxall and Ricketts 1983), we estimated that fat accounts for 78% of the daily mass loss in males. Although the respiratory quotient (RQ) of incubating Laysan Albatrosses is 0.68 (Grant and Whittow 1983), which suggests that they metabolize primarily fat, our estimates of the fat oxidized are considerably higher than the 55.5% generally used for calculating metabolic rate from changes in mass. Consequently, either more fat is oxidized during the incubation fast than has been previously assumed, or our measurements of $\dot{V}_{O_2}$ are unusually high.

The latter is a distinct possibility, especially since we measured $\dot{V}_{O_2}$ using a face mask. Jungius and Hirsch (1979) found, for example, that the heart rate of several species of seabirds, including the Waved Albatross (*D. irrorata*), increased significantly when humans approached them, although the birds often displayed no outward signs of disturbance. Although the albatrosses in our study appeared relaxed and we were out of sight in a tent during most of the experiment, it is nevertheless possible that simply wearing a mask may stress the birds, increasing their heart rates and elevating their metabolism.

The only direct measurements of metablism in incubating procellariiforms that we know of for comparison with ours are those of Grant and Whittow (1983) for Laysan Albatrosses (*D. immutabilis*) and Bonin Petrels (*Pterodroma hypoleuca*). The *resting* metabolic rates of these species are 256 and 645 kJ kg^{-1} day^{-1}, respectively. These values are close to the BMR predicted by the equation of Kendeigh et al. (1977) and within 10% of the BMR predicted from our own equation for procellariiforms (Adams and Brown, in press). During incubation, the metabolic rates of Laysan Albatrosses and Bonin Petrels are 119 and 500 kJ kg^{-1} day^{-1}, respectively. These values are lower than the predicted BMR and also lower than the metabolic rate predicted by Croxall (1982) for incubating procellariiforms, but his data were based on rates of mass loss. Grant and Whittow's (1983) results for incubating birds are also lower than our value for incubating Wandering Albatrosses, which was estimated using an equivalent technique, although they measured $\dot{V}_{O_2}$ with a metabolic chamber and a modified burrow system.

Weathers (1979) suggested that birds from temperate and tropical zones will be found to have lower metabolic rates than birds from cooler regions. The Laysan Albatross and the Bonin Petrel breed on the Hawaiian Islands, where ambient temperatures are considerably warmer than those at the sub-Antarctic breeding grounds of the Wandering Albatross. As a result, the metabolism of incubating adults and heat loss from their eggs may be less in the Hawaiian species, and consequently, the overall energetic costs to the parents during incubation also less than those of the Wandering Albatross.

Our results, coupled with Grant and Whittow's (1983), emphasize the need for further laboratory and field studies of procellariiforms, in which $\dot{V}_{O_2}$, RQ, and perhaps heart rates are measured simultaneously. Information about the body composition of these birds during incubation is also necessary before it will be possible to determine the true energetic cost of incubation for albatrosses.

ACKNOWLEDGMENTS

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FitzPatrick Institute, University of Cape Town, Rondebosch 7700, South Africa. Received 22 March 1983. Final acceptance 12 November 1983.

RECENT PUBLICATIONS

Wildfowl 34.—Edited by G. V. T. Matthews and M. A. Ogilvie. 1983. Wildfowl Trust, Slimbridge. 176 p. Paper cover. $15.00. Source: Administrative Officer, Wildfowl Trust, Slimbridge, Gloucestershire GL2 7BT, England. The latest issue of this annual (previously noticed in The Condor 85:248 and earlier) contains 21 articles about the behavior, reproduction, molt, populations, and other aspects of ducks and geese. Most of them concern wild birds and at least half deal with species that occur in the Americas. Since this series is essential for waterfowl biologists, they should note that copies of future issues will be printed only in sufficient numbers to meet known requirements. Those who wish to ensure a copy of the next year's issue should order and pay for it before 15 September 1984.

Censos de Aves en el Mediterraneo/Bird Census and Mediterranean Landscape. Proceedings of the VII International Conference on Bird Census, I[nternational] B[ird] C[ensus] C[ommittee], León, España 8-12 IX 1981.—Edited by F. J. Purroy. 1983. Universidad de León. 196 p. Paper cover. $4.50 postpaid. Source: Prof. F. J. Purroy Iraizoz, Catedrático de Zoología (Vertebrados), Universidad de León, León, Spain. Studies of bird distribution and abundance are currently following a variety of approaches, choosing methods and grid scales according to the objectives, resources, and preferences of the research teams. The IBCC meets biennially in order to report information and exchange ideas on such matters as the standards for censuses, the validity and applicability of various methods, and the comparability of data from different censuses. This volume contains the 35 papers on censusing or bird communities that were given at its 1981 meeting. While the majority of them deal with mediterranean habitats, the rest range afield, having been presented by delegates from 12 European countries plus the U.S. and Canada. The papers are in English or Spanish, each with a list of references and a summary in the other language. Maps, diagrams, and graphs. Avian community ecologists and atlas directors should find much of value here, particularly at such a bargain price.